

**Taxonomy, anatomy, and histology of the lined sea anemone,  
*Edwardsiella lineata* (Verrill, 1873)  
(Cnidaria: Anthozoa: Edwardsiidae)**

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*Abstract.*—The lined sea anemone, *Edwardsiella lineata* (Verrill, 1873) is a common inhabitant of shallow waters of the North Atlantic from Cape Cod to Cape Hatteras. Its larval form, described as *Edwardsia leidy* Verrill, 1898, is an endoparasite of the ctenophore *Mnemiopsis leidy* and has been identified as the cause of sea-bather's itch. Although the biology and anatomy of the larval form are well documented, the internal anatomy and histology of adults has not been described. Confusion about the correct name for this species and about the identity of adults that produce the larvae have made identifying and monitoring this species difficult. In this study, I describe the anatomy of adult members of *E. lineata*, synthesize existing accounts of its development and life history, and detail the taxonomy of *E. lineata* and the genus *Edwardsiella*.

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*Edwardsiella lineata* is the valid name for the species called *Fagesia lineata* (Verrill, 1873) and *E. leidy* Verrill, 1898. *Edwardsia leidy* is the larval form of *E. lineata* (Crowell 1965, 1976). Although the names of the larval and adult forms were synonymized (Crowell 1965, 1976), the larva continues to be cited as *E. leidy* (e.g., Gosner 1979, Kremer 1976, Meinkoth 1995). Even publications that recognize the synonymy fail to use the correct name for the species (e.g., Oviatt & Kremer 1977, Bumann & Puls 1996). Some of the nomenclatural confusion is probably caused by Crowell's (1976) acknowledgment that the generic assignment given in the synonymy was incorrect, as the genus *Fagesia* was under revision at the time (see Manuel 1981).

Although the anatomy, ontogeny, and ecology of the larval form are well characterized (e.g., Mark 1884, Crowell 1976, Crowell & Oates 1980, Bumann & Puls 1996), and the external anatomy of the adult is known (Verrill 1873), the internal anatomy and histology of adult *E. lineata*

are undocumented. The lack of information about internal morphology, and the absence of clear differential diagnoses for *E. lineata* and other western North Atlantic species in the family Edwardsiidae make identification and documentation of *E. lineata* populations difficult. Because *E. lineata* has been linked to sea-bather's itch in the North Atlantic (Freudenthal & Joseph 1992, 1993), documenting the distribution of this species is especially important.

#### Materials and Methods

For this study, I examined both live and preserved specimens of *E. lineata*. Live material was purchased from Marine Biological Laboratory (Woods Hole, Massachusetts); these specimens were collected by SCUBA divers in Cape Cod Bay (E. Enos, pers. comm.). Coloration and external anatomy were recorded prior to fixation. Freshly preserved material and museum specimens from the Yale Peabody Museum (YPM 7642 A1 and YPM 8802) and the United States National Museum, Smithson-

ian Institution (USNM 53363) were used for histological studies. Serial sections of paraffin-embedded preserved specimens were stained in Masson's Trichrome (Schreibman 1964).

In the following discussion of anatomy, "distal" refers to the oral disc and tentacles, "proximal" to the aboral end. The terms "dorsal" and "ventral" are used to describe the orientation of the retractor muscles and mesenteries (e.g., Carlgren 1921, Stephenson 1935, England 1987); more recent descriptions of actiniarian anatomy employ "sulcular" rather than dorsal, and "sulcar," rather than ventral (e.g., Stachowitsch 1992). I use the older terminology to facilitate comparison with descriptions of other edwardsiids; in no way is the use of the terms dorsal or ventral meant to homologize the longitudinal axis of actinarians with that of bilaterians.

Cnidae preparations were made by squashing approximately 1.0 mm<sup>2</sup> of tissue on a slide. Smears were prepared from tentacle, actinopharynx, mesenterial filament, and capitulum tissues from several individuals. Tissue smears were examined at 1000× magnification with differential interference optics. ScanPro measurement software (Jandel Scientific Software) was used to measure the length and width of undischarged cnidae capsules projected onto a Summa Sketch digitizing pad tablet (Summagraphics). Cnidae nomenclature follows Mariscal (1974).

Cnidae presentation is modified from Dunn et al. (1980). The capsule with the smallest (or greatest) width is generally not the capsule with the smallest (or greatest) length. Summarizing the range using four measurements, providing a length by width range, as is typical in cnidarian taxonomy, is imprecise (Fautin 1988) and can imply capsule sizes not observed. I present the range by citing the size of the shortest, narrowest, longest, and widest capsule separately. The sizes of these capsules define a space that includes the size coordinates of all observed cnidae.

## Systematic Account

Family Edwardsiidae Andres, 1883

Genus *Edwardsiella* Andres, 1883

Edwardsiidae with column differentiated into capitulum, scapus, and scapulus, three or more cycles of tentacles. Tentacles hexamerously arranged, those of innermost cycle longest. Capitulum with ridges; nematocysts of capitulum concentrated on ridges. Scapus bears periderm but lacks nemathybores and tenaculi. Aboral end not differentiated into a physa. Ciliated tracts of filament short, discontinuous (modified from Stephenson 1935, Carlgren 1949, Manuel 1981).

*Edwardsiella lineata* (Verrill, 1873)

Figs. 1–3

*Edwardsia lineata* Verrill, 1873:421.—Verrill & Smith, 1874:445.—Parker, 1900:750.—Hargitt, 1912:248.—Miner, 1950:198.—Williams, 1981:350.

*Edwardsia leidy* Verrill, 1898:496.—Parker, 1900:750.—Hargitt, 1912:248.—Miner, 1950:198.—Gosner, 1971:154.—Kremer, 1976:213.—Oviatt & Kremer, 1977:236.—Gosner, 1979:95.—Williams, 1981:349.

*Edwardsia* sp. Verrill & Smith, 1874:504.—Mark, 1884: pl. xii.

*Edwardsiella lineata* Pratt, 1935:151.—Freudenthal & Joseph, 1992:101; 1993:542.

*Edwardsia* sp. Mark Carlgren, 1949:23.

*Fagesia lineata* Carlgren, 1949:25.—Gosner, 1971:153.—Crowell, 1976:247.—Crowell & Oates, 1980:139.—Sebens, 1998:20.—Williams, 1981:350.—Shick, 1991:253.—Meinkoth, 1995:352.—Weiss, 1995:4.14.

*Adult external morphology.*—Body translucent white, with pale tan lines indicating mesenterial insertions. Mesenterial compartments proximal to capitulum streaked with opaque white. Oral cone prominent, opaque white. Tentacles marginal, filiform, 18–36, in 2–3 cycles, 6 tenta-



Fig. 1. External anatomy of preserved specimen of *Edwardsiella lineata* (USNM 53363). Scale bar = 3.0 mm.

cles of innermost cycle longest. Tentacles translucent white with opaque white flecks, each may bear longitudinal opaque mark on oral side.

Column 10–30 mm long, 2–5 mm in diameter, divisible into 2 distinct regions: short, ridged, capitulum and long, smooth, scapus covered by rough periderm of mucus, detritus, and sand grains (Fig. 1). Periderm sheath-like, not attached to column by suckers or tenaculi, extending from scapus to aboral end; contracted specimens appear entirely enclosed by periderm. Aboral end not ampullaceous, instead tapering or slightly rounded, with rugae, but without cinclides or central invagination.

*Internal anatomy.*—Actinopharynx tan, partially visible through body wall. Six pairs mesenteries in primary cycle: two pairs of directives and four pairs, each of which has one member complete and fertile (= macrocneme) and one member minute, imperfect, sterile (= microcneme). Secondary and tertiary cycles, when present, microcnemous; all microcnemes restricted to distal capitulum. Single ventral siphonoglyph. Trilobed ciliated filaments short, discontinuous, present in region proximal to actinopharynx and in reproductive tract; gonochoric, oviparous.

Retractor muscles large, circumscribed, convex (Fig. 2A, B), with closely spaced branches of variable height on both sides of mesenterial lamella. Retractor branch height generally decreases toward coelenteron; branches both simple and ramified, with ramified branches toward edges of muscle (Fig. 2A, C). Parietal muscle strong, circumscribed, symmetrical, trefoil-shaped, with central mesogleal lamella thicker than lateral branches. Fibers of parietal muscle extend onto body wall, beyond profile of lower parietal branches.

Ectoderm of scapus columnar, glandular, with groups of basitrichs. Thickness of mesoglea and ectoderm varies in capitulum: mesoglea and ectoderm thickest in center of mesenterial compartment, tapering towards

mesenteries, forming capitular ridges. Ectoderm contains thin processes of mesoglea.

*Cnidom.*—Spirocysts, microbasic *b*-mastigophores, basitrichs, and microbasic *p*-mastigophores (Fig. 3). See Table 1 for distribution and size information.

*Larval morphology.*—Young larva pinkish-tan, ciliated. Shape very changeable, most commonly ovoid, can be spheroid or vermiform. Parasitic juvenile 2.0–3.0 mm long, approximately 1 mm in diameter, translucent pink, with 4–8 tentacles (Mark 1884, Crowell 1976). Larva becomes shorter and thicker after leaving host (Mark 1884, Crowell 1976).

*Development, distribution, and natural history.*—Although position of each mesentery in larval coelenteron prefigured by furrow in endoderm (Mark 1884), mesenteries develop from evaginations of endoderm (Mark 1884). Mesenterial folds ciliated. Ventrolateral mesenterial pairs arise first, followed by dorsolateral, ventral and dorsal mesenteries (Mark 1884). Mesenteries more developed distally than proximally. Muscles develop after all pairs present (Mark 1884).

Found along North Atlantic coast of North America, from Cape Cod, Massachusetts to Cape Hatteras, North Carolina. Littoral to sublittoral. Adults commonly inhabit rock crevices, *Zostera* root mats, or boreholes created by mollusks, worms, or sponges. Groups of *E. lineata* form mat-like “colonies,” with individuals sharing periderm. Adults asexually reproduce through transverse fission (Crowell & Oates 1980).

Juvenile *E. lineata* parasitize the ctenophore *Mnemiopsis leidyi* (see Crowell 1965, 1976). Multiple larvae infest a single host. Larvae enter the ctenophore through the ectoderm and migrate through the canal system and mesoglea to the pharynx (Crowell 1976, Bumann & Puls 1996). The oral end of the larva protrudes into the stomodeum of host (Crowell 1976, Bumann & Puls 1996); the larva removes food passing through host pharynx.

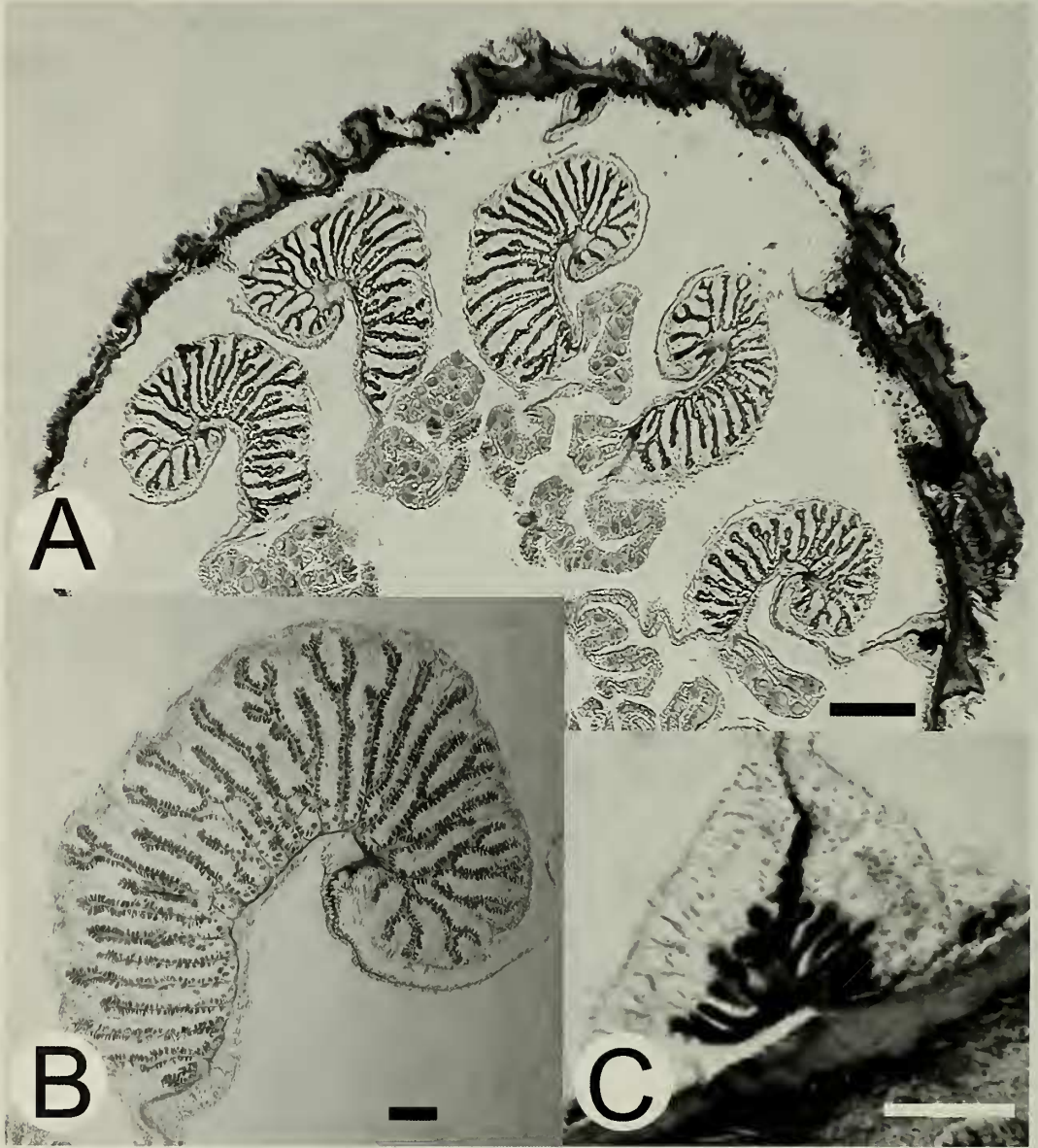


Fig. 2. Internal anatomy of *Edwardsiella lineata*. A. Cross section through column midline. B. Cross section through retractor muscle. C. Cross section through parietal muscle. Scale bars: A = 200  $\mu\text{m}$ ; B, C = 50  $\mu\text{m}$ .

### Discussion

*Taxonomy.*—The taxonomic history of the genus *Edwardsiella* is extremely convoluted. Andres (1883) erected *Edwardsiella* for edwardsiids with 20 or more tentacles. He listed the nominal species in no apparent order and did not name or imply

a type species. Carlgren (1892, 1893) described a new genus, *Milne-Edwardsia* (later spelled *Milneedwardsia*), and altered the definitions of *Edwardsia* and *Edwardsiella* to emphasize tentacle arrangement and the arrangement of nematocyst-filled hollows in the ectoderm and mesoglea). According to Carlgren (1892,

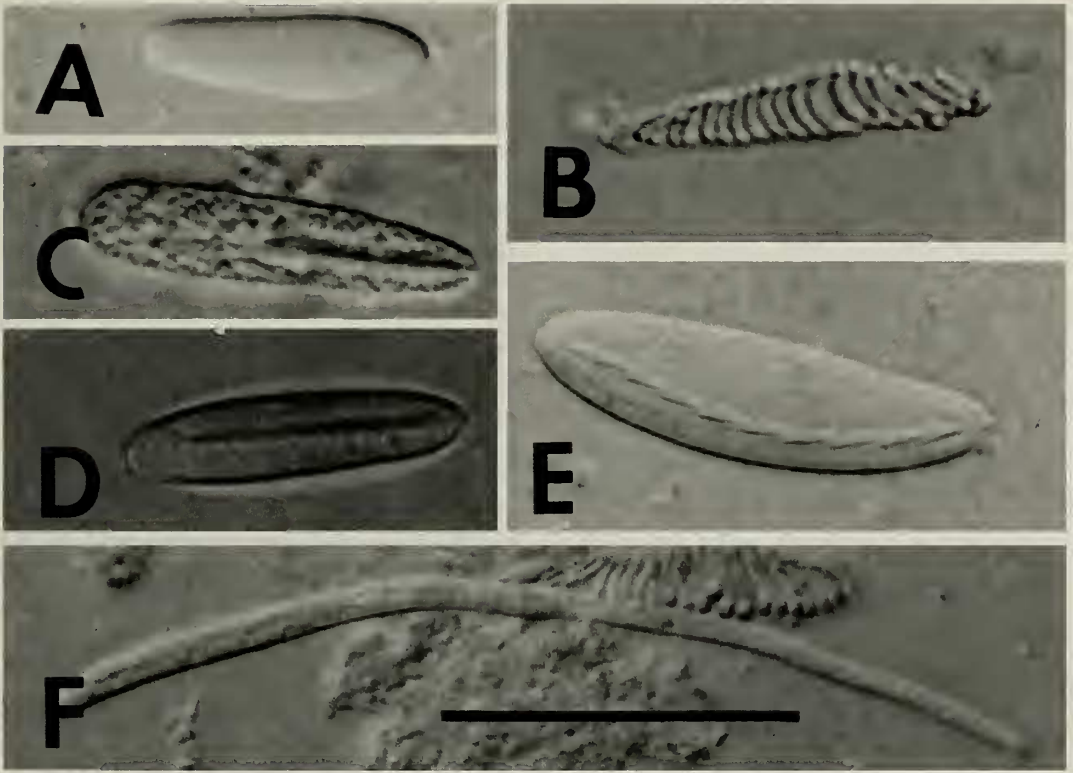


Fig. 3. Representative cnidae from *Edwardsiella lineata*. (Refer to Table 1 for specific size information.) A. Spirocyst. B. Microbasic *b*-mastigophore. C. Basitrich. D. Microbasic *p*-mastigophore. E. Microbasic *b*-mastigophore. F. Basitrich. Shape of these basitrichs varies from s-curve to straight. Scale bar = 20  $\mu\text{m}$ .

1893), *Edwardsiella* and *Edwardsia* were characterized by nemathybomes and octamerously arrayed tentacles; *Milneedwardsia* had no nemathybomes and had hexamerously arrayed tentacles. *Edwardsiella* differed from *Edwardsia* in tentacle number and nemathybome arrangement (Carlgren 1893). Although Carlgren's (1892, 1893) definition of *Edwardsiella* was followed by a few authors (e.g., McMurrich 1913, Verrill 1928), the name was generally not used. Carlgren (1921) later submerged *Edwardsiella* within *Edwardsia*.

*Milneedwardsia* was found to be preoccupied, and the genus was renamed *Fagesia* (Delphy, 1938). In his catalog of Actiniaria, Corallimorpharia, and Ptychodactiaria, Carlgren (1949) listed *Milne-Edwardsia loveni* as the type of *Fagesia*. However, in the earlier of Carlgren's two descriptions

for *Milneedwardsia*, *M. loveni* is a nomen nudum. *Edwardsia carnea* Gosse, 1856 was the only valid species in *Milneedwardsia* at the time of description and is, therefore, its type species by monotypy.

In the time between the description of *Milneedwardsia* and the discovery that *Fagesia* was preoccupied, the four species initially assigned to *Edwardsiella* were transferred to other genera or synonymized, and the name fell out of general use. In his monograph on British anthozoans, Manuel (1981) resurrected *Edwardsiella* as a replacement name for *Fagesia*, and named *E. carnea* as the type of *Edwardsiella* Andres, 1883. Although Manuel cited monotypy as the rationale for this action (because *E. carnea* was the last species left in *Edwardsiella*), it is actually type fixation due to subsequent elimination. Although subsequent

Table 1.—Size ( $\mu\text{m}$ ) and distribution of cnidae in *Edwardsiella lineata* (letters refer to Fig. 3).  $n$  = number of capsules measured;  $N$  = proportion of animals examined bearing each type of cnida.

Tissue	Cnida type	$n$	$N$	Capsule of smallest length	Capsule of smallest width	Capsule of greatest length	Capsule of greatest width
Tentacle	Spirocyst (A)	119	6/6	13.0 by 1.7	13.0 by 1.7	29.5 by 4.1	27.7 by 6.0
	Microbasic <i>b</i> -mastigophore (B)	288	6/6	7.8 by 2.6	9.4 by 1.6	32.1 by 6.5	31.0 by 8.7
	Basitrich (C)	112	6/6	12.1 by 2.9	12.8 by 2.4	23.3 by 4.4	18.6 by 5.0
Capitulum	Microbasic <i>b</i> -mastigophore (E)	195	6/6	24.9 by 5.9	27.9 by 4.9	40.1 by 7.2	30.9 by 9.1
	Basitrich (C)	78	6/6	13.6 by 3.2	19.3 by 2.1	20.1 by 3.2	16.9 by 4.9
Actinopharynx	Microbasic <i>p</i> -mastigophore (D)	170	6/6	14.0 by 4.1	19.7 by 3.7	37.3 by 5.9	28.9 by 7.8
	Microbasic <i>b</i> -mastigophore (E)	155	6/6	7.8 by 2.3	10.5 by 1.8	40.9 by 6.7	40.9 by 6.7
Filament	Microbasic <i>p</i> -mastigophore (D)	273	7/7	22.2 by 3.4	25.0 by 2.9	31.8 by 6.1	26.5 by 9.3
	Basitrich (F)	35	5/7	31.1 by 2.1	34.4 by 1.8	48.0 by 2.8	48.0 by 2.8

elimination is not sufficient for elevating a species to type status, Manuel's declaration of *E. carnea* as the type, coupled with subsequent elimination, is a valid type designation (Articles 6.9.1 and 6.9.4; ICZN 1999). Because *E. carnea* is also the type of *Milneedwardsia*, *Edwardsiella* is the senior objective synonym for *Milneedwardsia* and *Fagesia*. *Edwardsiella* comprises five nominal species: *E. carnea* (Gosse, 1856), *E. ignota* (Carlgren, 1959), *E. janthina* (Andres, 1881), *E. lineata* (Verrill, 1873), and *E. loveni* (Carlgren, 1893).

The combination *Edwardsiella lineata* has been used three times. This combination has not appeared in any general taxonomic, ecological, or experimental publication. The first citation of the correct combination was based on a misinterpretation of the literature. Pratt (1935) placed *E. lineata* in *Edwardsiella* based on Andres' (1883) generic criteria, rather than following Carlgren's (1892, 1893) redefinition. The more recent uses appeared in medical journals (Freudenthal & Joseph 1992, 1993) and have not been cited by taxonomic workers.

*Similar species*.—Members of the family Edwardsiidae can be distinguished from most other sea anemones by their long, thin column, and by the number and arrangement of mesenteries. Edwardsiid adults have eight fertile, perfect macrocnemes and a variable number of imperfect, minute microcnemes just below the oral disc. *Edwardsiella* is the only genus of Edwardsiidae whose members generally do not burrow; members of this genus typically live in crevices, in dead coral skeletons, or in mats on the substrate. *Edwardsiella lineata* is the only North American species of *Edwardsiella*. It shares a ridged capitulum, tapering aboral end, periderm-covered column, and relatively wide nematocysts in the tentacles with other species of *Edwardsiella*.

Three species of edwardsiids co-occur with *Edwardsiella lineata* in the western North Atlantic: *Edwardsia elegans* Verrill,

1869, *Nematostella vectensis* Stephenson, 1935, and *Drillactis pallida* (Verrill, 1880). *Edwardsia elegans* normally has 16 tentacles; *Edwardsiella lineata* has 18 or more. These two species can be further distinguished by differences in column morphology. *Edwardsia elegans* has an unridged capitulum, conspicuous nemathybomes on the middle and lower column, and a naked, bulbous aboral end; *Edwardsiella lineata* has a ridged capitulum, a smooth mid and lower column, and a tapering, periderm-covered aboral end. *Nematostella vectensis* and *E. lineata* differ in tentacle number, size, and color: *N. vectensis* has 16 tentacles and is generally small (<10 mm), opalescent white or translucent. Furthermore, the coelenteron of *N. vectensis* contains nematosomes, ciliated spherical nematocyst bodies (Stephenson 1935). *Drillactis pallida*, which has been reported only once (the specimens cited in Verrill 1928 and Carlgren 1950 are from the type collection, described in Verrill 1880), is similar in size and external appearance to *E. lineata*. However, in *D. pallida*, the inner tentacles are shorter than the outer tentacles and the retractor muscles are smaller and less complex than those of *E. lineata*. Furthermore, *D. pallida* lacks nematocysts on the capitulum, and possesses nematosomes (pers. obs.).

*Unusual aspects of the species.*—The mesenterial filaments of *E. lineata* contain long, thin basitrichs (Fig. 3F, called pencilli B<sub>1</sub> by den Hartog 1987).

Although these nematocysts are recorded from other actinarians (e.g., Hand 1955, den Hartog 1987, Belém & Pinto 1990, Riemann-Zürneck & Gallardo 1990), they have not been reported in Edwardsiidae, and their distribution in the Actinaria is poorly understood. Because these basitrichs are more rare than other types of cnidae in the filament, and are unlike other nematocysts in general shape, they may have been overlooked in other species. Furthermore, these nematocysts are often broken or bent

in squash preparations, making it less likely that they will be recognized and recorded.

The life history of *Edwardsiella lineata* has two unusual features: parasitism and transverse fission. Parasitism on medusae is seen in several burrowing anemones. Species in the genus *Peachia* (family Haloclavidae) parasitize hydromedusae (Nyholm 1949, Spaulding 1972); in fact, Carlgren (1949) regarded this as a diagnostic feature of *Peachia*. *Edwardsiella lineata* is the only edwardsiid known to parasitize medusae, although larvae of *E. carnea* may be associated with the ctenophore *Bolinopsis* (see Stephenson 1935).

Transverse fission is reported in only a few actinarians, including the edwardsiid *Nematostella vectensis* (Crowell & Oates 1980, Shick 1991, Hand & Uhlinger 1992). Members of no other edwardsiid species are known to undergo regular asexual reproduction. Individuals of both *Edwardsiella lineata* and *N. vectensis* often live in dense aggregations (pers. obs., Crowell & Oates 1980, Hand & Uhlinger 1994), presumably the result of asexual reproduction. The dispersal ability afforded *E. lineata* larvae by the association with ctenophores may be especially important because of the tendency of this species to form dense mats that cover locally available substrate.

*Edwardsiella lineata* has been suggested as a possible biocontrol agent for *Mnemiopsis leidyi* introduced into the Black Sea. *Edwardsiella lineata* compromises growth and survival of *M. leidyi* and may have a long-term effect on the population size of *M. leidyi* (Crowell 1976, Kremer 1976, Bumann & Puls 1996). However, the life history of *E. lineata* suggests that an introduction of this species may have undesirable consequences. The larvae cause sea-bather's eruption, an unpleasant dermatitis that may render beaches temporarily unfit for recreational use (Freudenthal & Joseph 1993). Predators of adult *E. lineata* are unknown, as is the role this species plays in the ecology of benthic communities. Because *E. lineata* is capable of asexual re-



production and tends to occur in high numbers when present, this species could itself become invasive, compounding the problem of introduced species in the Black Sea, rather than solving it.

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